EVIDENCE FOR UNPALATABILITY IN THE GENUS *DELIAS* HÜBNER (LEPIDOPTERA: PIERIDAE) AND ITS ROLE IN MIMETIC ASSEMBLAGES

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Abstract

Evidence is presented which strongly suggests that butterflies of the pierine genus *Delias* Hübner are highly distasteful or even toxic to vertebrate predators, but may be consumed without ill effects by invertebrate predators. The role of *Delias* species as models for Batesian and Mullerian mimetic assemblages is discussed, with particular reference to the probable Batesian mimics of the genus *Mynes* Boisduval. It is suggested that the inexact resemblance of Batesian mimics of *Delias* is due to their fluttering flight, which transmits a distinctive flash pattern but few fine details of colour and pattern. A similar argument provides an explanation for the lack of discernible Mullerian assemblages in the genus. The relatively few mimics of *Delias* may also be a result of the probable Gondwanan origin of the genus and its present day preference for temperate or montane climates, which has meant there has been insufficient contact with potential mimics from the Oriental fauna for many associations to form.

Introduction

The mimetic resemblances of butterflies of the genus *Delias* Hübner and other pierids, notably *Cepora* Billberg and the nymphalid genus *Mynes* Boisduval are well known (Dixey 1918). However the true nature of the relationship has never been clarified. Certain evidence, direct and circumstantial, suggests that *Delias* species, almost all of which feed in the larval stage on mistletoe (Loranthaceae), are distasteful or even toxic to vertebrates, are aposematically patterned as adults and may serve as the focus for Batesian and/or Mullerian assemblages throughout their geographic range. To date however there has been no hard evidence, by way of chemical analysis or bioassay, that these butterflies are unpalatable and evidence for the chemical basis of toxicity based on the hostplant chemistry is also ambivalent (Samuelsson 1966, 1969). In this paper I present some new evidence that *Delias* species are unpalatable or toxic to vertebrates, but probably palatable to invertebrates. This is provided by direct observation of predation and rejection in the field and by a simple experiment. I also review patterns of apparently *Delias*-centred mimetic assemblages which occur throughout the geographic range of the genus. In particular, I examine the relationship between *Delias* and *Mynes*, many species of which appear to be Batesian mimics of various *Delias* species

Circumstantial evidence of unpalatability

The larvae of *Delias* are exposed and gregarious and presumably vulnerable to predation. While none of the Australian species is especially colourful, they are not cryptic. Larvae of some Oriental species such as *D. henningia* Eschscholtz are strikingly patterned with dark brown and yellow bands. Pupae are characteristically bright yellow and not concealed. The adults are slow flying and conspicuous. Moreover, the undersides of most species are very brightly coloured, making them extremely conspicuous when at rest.

The butterflies roost quite openly. Although occasionally I have seen beak marks on a high proportion of specimens, I have very seldom seen the characteristic symmetrical damage caused by birds or other vertebrate predators attempting to take the insect while at rest. This negative evidence is based on many hundreds of observations on *D. nigrina* (Fabricius) and *D. argenthona* (Fabricius), which are present for most of the year in large numbers in my garden at Caloundra, Queensland. Similar observations apply to over 300 specimens of more than 50 species I have collected in Papua New Guinea and Southeast Asia.

General evidence of rejection by vertebrates

Direct evidence of avian predation is often very difficult to obtain. For example Robbins (1980), in an extensive investigation of the role of avian predation in the evolution of "false heads" in lycaenids, did not witness a single attack in a two year study. It is to be expected that attacks on distasteful species would be even less frequently observed. I first began observing *Delias* seriously in 1974 and have, in the 25 years since, watched many thousands of individuals. The following observations are the total of interactions with predators I have witnessed in that time.

In late September 1987 a young Lewin's honeyeater (*Meliphaga lewinii*) fairly recently fledged from a nest in my garden, was observed taking a *D. argenthona* male in flight. It held it by the body for about 25 seconds, then released it intact but badly injured. A few days later a similar interaction between a spangled drongo (*Dicrurus hottentottus*) and a male *D. nigrina* was observed. As indirect evidence of avoidance, about the same period I sampled 30 male *D. nigrina* and 10 male and female *D. argenthona.* Of these, nine (23%) had beak marks on their wings, including two *D. argenthona* and one *D. nigrina* which had symmetrical damage indicating they had been attacked at rest. At that time many newly fledged insectivorous birds were about. I took another sample of the same size three weeks later in mid October, by which time none of the specimens showed any sign of attack suggesting the young birds were rapidly educated to avoid them. It should be noted that the maximum lifespan of *D. nigrina* in the wild at this time of year seldom exceeds two weeks (Orr 1988) hence this sample would have mostly represented a later brood of butterflies. In March 1978 a Lewin's honeyeater, which was feeding on insects at the time, was seen to fly within 20 cm of a resting *D. argenthona*, apparently investigate it briefly, then fly off. In April 1985 little wattlebirds (*Anthochaera chrysoptera*) were twice observed to fly swiftly and deliberately at fluttering *D. nigrina* males, only to pull out of the attack at the last moment, swerving abruptly when about 30 cm from the butterfly. In neither case did the butterfly take any evasive action before or after the aborted attack. In January 1979 spinetailed swifts (*Hirundapus caudacutus*) were seen swooping down from a great height and snatching various butterfly species which were hilltopping on Gunong Jassar, West Malaysia. Twice I saw an apparent attack on *Delias* *pasithoe parthenope* (Wallace), where the bird swerved at the last moment, much as described above.

In an outdoor insectary small populations of *D. argenthona* and *D. nigrina* were maintained for over a year where at night they roosted communally on the walls. Small garden skinks, which frequently captured and ate small to medium sized lycaenids and satyrids, including *Melanitis leda bankia* (Fabricius), were on three occasions observed to attack roosting *Delias*, grasping them by the thorax or abdomen, but releasing them after a few seconds.

Experimental evidence of the distastefulness or toxicity

In 1996, a magpie (*Gymnorhina tibicen*) regularly came into my house to accept scraps of meat, *Spodoptera* Guenée larvae and various geometrid larvae from plants believed to be low in noxious chemicals. These were always eaten enthusiastically. When it was offered mature *Delias nigrina* larvae it swallowed the first avidly, then took another somewhat less willingly, but after about five minutes showed visible signs of distress, flew to a nearby branch and vomited. It was only after some days and much coaxing that it returned to feed and, when offered unadulterated mince, ate it enthusiastically, but when offered pieces of mince mixed with freshly ground adult *D. nigrina* or *D. argenthona*, it briefly tasted them then rejected them. The Magpie was almost certainly a naïve subject, since its ordinary method of feeding would not have brought it into contact with either larval or adult *Delias*. Clearly this is not statistical proof of unpalatability of *Delias*, being based on a sample size of one, but taken in conjunction with other evidence it does suggest a strong *prima facie* case for distastefulness in adult and larval stages.

Further evidence is provided by a simple investigation of the reponses of wattlebirds (*Anthochaera chrysoptera*) to *Delias* larvae presented at a feeding table to which they had become habituated. When palatable *Spodoptera* larvae were offered, they were eaten, whereas the *Delias* larvae of similar size and colour were sometimes investigated but never taken. When both types of larvae were presented only the *Spodoptera* were taken.

Palatability to invertebrate predadators:

There is no evidence that *Delias* are unpalatable to invertebrate predators. Between 1982 and 1988 I maintained captive populations of up to 12 *D. nigrina* and/or *D. argenthona* in a large outdoor insectiary at Caloundra. Both species were regularly taken and eaten by *Thomisus* Walkenauer sp. (Araneae: Thomisidae), living in flowerheads. On one occasion an unidentified preying mantis captured a *D. nigrina* female, which it consumed normally and without ill effect. A more critical test was provided by *Nephila* Leach sp. (Araneae: Argiopidae), which reject or partially reject any butterfly feeding on Apocynaceae, presumably on account of sequestered pyrrolizidine alkaloids (Brown 1984), as well as *Aristolochea* feeding troidine swallowtails. *Nephila* showed no tendency at all to reject *D. argenthona* or *nigrina* (n=34). It is worth noting that *Danaus affinis* (Fabricius) bred on *Ischnostemma carnosum* and *Euploea core* (Cramer), which had fed on *Ischnocarpus frustescens,* both asclepiadaceous foodplants rich in cardenoloids but lacking P.A.s, were also eaten by *Nephila*, but they rejected *E. core* which had fed on *Parsonsia straminea* (Apocynaceae), which does contain P.A.s (Orr *et al.* 1996).

Evidence of Batesian mimicry

When on the wing, butterflies of the genus *Mynes*, especially the females, bear a striking resemblance to *Delias*, particularly to members of the *D. nigrina* group. It must be stressed that in terms of details of pattern they are quite imprecise mimics. But exact resemblance may not be necessary as both *Mynes* and *Delias* share a constantly fluttering mode of flight, as opposed to the sailing flight of many danaids and heliconiids which reveals clear details of pattern and colour when the butterfly is on the wing. The flash pattern transmitted by *Mynes* can be very deceptive. *Mynes* species feed on various Urticaceae, which are usually associated with palatability.

M. geoffroyi guerini Wallace is found in northeastern Australia where its distribution and habitat preferences overlap with those of *Delias nigrina.* In flight, the female strongly resembles the female of *D. nigrina* (cf Common and Waterhouse 1972). Males vary in their underside coloration, but the darker forms likewise appear to mimic the male of *D. nigrina.* This species is evidently the frequent target of unsuccessful attacks by birds. For example in a series of 37 *M. geoffroyi guerini* I collected in southern Queensland, 14 (38%) had large pieces missing from the wings suggestive of avian attack. Ten of these were males of the pale form (59% of all males, n=17), which are not obvious mimics. In most cases only one wing was damaged, indicating that the attack probably took place while the butterfly was flying. A high incidence of wing damage is a well known characteristic of Batesian mimics, presumably resulting from tentative attacks by birds. By contrast, in a series of 83 *D. nigrina* collected at the same times and places as the *Mynes*, only two showed faint beak marks and none had large pieces of wing missing.

Moreover more than half the known *Mynes* species have a general coloration similar to syntopic *Delias* species, at least in the female (Table 1). Where both sexes are mimetic, the male and female *Mynes* exhibit the same upperside coloration as the corresponding sex of the putative *Delias* model. Striking parallels occur - for example the underside of the hindwing of *Delias madetes* (Godman & Salvin) from New Britain is extensively yellow with a bright red costal streak and this pattern is mirrored in *Mynes eucosmetos* Godman & Salvin from the same locality. Table 1 is by no means comprehensive in its listing of *Mynes* forms or potential models and it is clear that field observations are required to support the suggested associations (see Parsons 1992, 1999).

Table 1. Possible Batesian associations.

Putative model	putative mimic	distribution
Delias nigrina (Fabricius) (female/ male)	*Mynes geoffroyi guerini* Wallace (female/ male dark form)	Eastern Australia
Delias ornytion (Godman & Salvin)	*Mynes geoffroyi ogulina* Fruhstorfer (female/ male dark form)	New Guinea lowlands
Delias ladas Grose-Smith	*Mynes geoffroyi ogulina* Fruhstorfer (female/ male dark form)	New Guinea highlands
no obvious model	*Mynes geoffroyi* (Guérin-Méneville) (male pale form)	Australia, NG lowlands & highlands
Delias duris Hewitson	*Mynes doubledayi* Wallace	Ceram
Delias funerea Rothschild ?	*Mynes plateni* Staudinger	Halmahera
No obvious model	*Mynes halli* Joicey & Talbot	New Guinea highlands
No obvious model	*Mynes websteri* Grose-Smith	New Guinea highlands
No obvious model	*Mynes woodfordi* Godman & Salvin	Solomon Is
Tellervo Kirby sp.	*Mynes anemone* Vane-Wright	New Guinea lowlands
Tellervo Kirby sp.	*Mynes katherina* Ribbe (male)	New Britain
Delias totilla Heller	*Mynes katherina* Ribbe (female yellow form)	New Britain
Delias madetes (Godman & Salvin) ? or *Delias salvini* Butler	*Mynes eucosmetos* Godman & Salvin	New Britain / New Hannover
Delias eschatia Joicey & Talbot/ *Delias vidua* Joicey & Talbot	*Mynes talboti* Juriaanse & Volbreda	Buru

Much closer resemblances occur also between certain syntopic *Cepora*, *Prioneris* Wallace and *Delias* species in New Guinea, Indonesia and Malaysia. Many examples of strong geographic correspondence in pattern and colour, apparently centred on a *Delias* model, are figured by Dixey (1920). But as the Capparidaceae feeding *Cepora* and *Prioneris* may also be to some extent distasteful, it is uncertain if we can ascribe such convergences to Batesian mimicry, or to a weak Mullerian association (see Turner 1984). Both genera are mostly somewhat faster flying than *Delias*, but the distinction is not a strong one and in my experience similarly patterned species of all three genera are easily mistaken.

Certain montane Satyridae in New Guinea appear to mimic *Delias* species. In particular *Erycinidia virgo* (Rothschild & Jordan) and *E. dulcis* (Jordan) are slow flying generalized mimics of the *Delias aroae-cunningputi* group (Parsons 1988). It should again be noted that these are not very good mimics in terms of wing pattern, but they have evolved a general coloration and mode of flight which makes the similarity striking when seen in nature.

Other species of *Erycinidia* Rothschild & Jordan, such as *E. hemileuca* Jordan, resemble syntopic *Delias* species on the upperside but not on the underside and as they are very rapid in flight they are probably not mimetic. In Southeast Asia both sexes of the satyrids *Elymnias vasudeva* Moore and females of *E. esaca* (Westwood) mimic *Delias pasithoe* (Linnaeus) or *D. ninus* (Wallace) which they strongly resemble in flight (Corbet and Pendlebury 1992). Most other species of the genus mimic Danaidae.

Evidence of Mullerian mimicry

Apparently *Delias* are only rarely involved in clear Mullerian associations. It is probable that certain species of Southeast Asian *Cyclosia* Hübner (Zygaenidae) are Mullerian mimics of *Delias*. Zygaenidae typically feed on cyanogenic plants and are considered unpalatable (Scoble 1992). There is no evidence of Mullerian assemblages forming within the *Delias*. In New Guinea a few convergences do occur, but this appears to be an incidental consequence of intense speciation among closely allied forms. There is no reason to expect the distinctive patterns on the underside to be maintained by sexual selection, which might be suggested as a source of diversification of colour patterns opposing the formation of Mullerian rings. Firstly, they are not generally sexually dimorphic on the undersides; secondly, courting males expose the upperside of their wings to the female (Orr 1988), presumably wafting a species-specific androconial secretion over her; and thirdly, closely allied species with nearly identical underside wing markings, such as *D. isocharis* Rothschild & Jordan, *D. ligata* Rothschild and *D. kummeri* Ribbe, fly in the same localities on Mt Kiandi, without apparent hybridisation. There is a definite tendency for all *Delias* species occurring at high altitudes to be very dark, but this is surely a developmental effect due to low temperatures or an adaptation to allow maximum absorption of the scarce sunlight. Despite this lack of convergence in pattern, *Delias* in any given locality in the New Guinea highlands are very difficult to tell apart on the wing and are generally perceived in general terms as light coloured species, yellowish species, dark species and so on. Perhaps with their fluttering flight they are sufficiently similar to one another for a Mullerian selective advantage to be operating without the development of obvious Mullerian resemblances which are apparent to us in the pinned specimen.

Discussion

Although it seems likely that *Delias* species sequester toxic compounds, the chemical nature of these must remain uncertain. The mistletoes, at least those of the family Viscaceae, are known to contain potent cardioactive compounds (Samuelsson 1962). This is apparently the source of the supposed magical properties attributed to the plant by Celtic druids. Active compounds isolated include choline and γ-amino butyric acid, but most significant toxic substances are complex polypeptides (viscotoxin). In Australia *Delias* species feed naturally on members of both families of mistletoe, with the Loranthaceae dominating. Samuelsson (1966, 1969) did not find viscotoxins in European members of this family, but as our understanding of mistletoe chemistry is clearly incomplete, this should not be taken as evidence of a lack of toxicity in Australian region species. However, even if we assume that complex toxic compounds confer toxicity on the insects which feed on them, it is still unclear if these are sequestered directly, or are in some way modified to form secondary protective toxic substances.

As the *Delias* appear to be strongly aposematic, questions must be asked such as why do they not attract high quality Batesian mimics, why are so few *Delias* species involved as models and why is there no obvious development of well defined Mullerian rings? The answers to these questions are probably twofold. Firstly, as discussed above, since *Delias* constantly flutter an approximate mimetic resemblance in coloration is probably effective as long as the correct flight pattern is adopted. The efficacy of an approximate resemblance will also tend to prevent the formation of obvious Mullerian rings. Secondly, the *Delias* are very probably of Gondwanan origin, adapted largely to temperate or montane rainforest. Only a handful of other butterflies which belong to potentially mimetic groups are of similar origin and currently occur in the same types of habitats as *Delias*. *Mynes* is an Australian region genus of uncertain affinities which does overlap broadly with some *Delias* in habitat preferences and the two genera have probably existed together for a very long time. The montane satyrid genus *Erycinidia* may also be of southern origin. The remainder of the common Batesian mimetic groups, such as *Hypolimnas* Hübner and *Elymnias* Hübner, are of Oriental origin and may simply not have coexisted for long enough with the few species of *Delias* which have established themselves in the tropical lowlands for associations to develop, especially as most species in these genera were already Batesian mimics of the very differently patterned danaine genera. Moreover, these same danaiines are already largely involved in Mullerian associations with each other (Ackery and Vane-Wright 1984) and convergence toward the vastly different pattern and mode of flight of *Delias* is unlikely. This postulated historical effect could be tested by examining other probable mistletoe feeding Pieridae, *Mylothris* Hübner in Africa and *Archonias* Hübner (?), *Catasticta* Butler, *Pereute* Herrich-Schaeffer, *Charonius* Röber (?) and *Leodonta* Butler (?) in South America (see DeVries 1987) to determine if they are more closely involved in mimetic associations than are *Delias*. A perusal of D'Abrera (1978, 1981-94) suggests this may be the case.

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